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Size-related shifts in the habitat associations of young-of-the-year winter flounder (*Pseudopleuronectes americanus*): field observations and laboratory experiments with sediments and prey

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Abstract

Field surveys and laboratory studies were used to determine the role of substrata in habitat selection by young-of-the year winter flounder. A synoptic field survey of winter flounder and sediments in the Navesink River–Sandy Hook Bay estuarine system in New Jersey demonstrated that winter flounder distribution was related to sediment grain size. Analysis using a generalized additive model indicated that the probability of capturing 10–49 mm SL winter flounder was high on sediments with a mean grain diameter of ≤ 0.5 mm, while fish 50–95 mm were least likely to be collected on fine sediments and most commonly on sediments with a grain-size near 1.0 mm. In the laboratory, sediment preferences and the burying ability of winter flounder (15–69 mm SL) were tested by exposing fish in 10-mm size groups to a choice of azoic sediments of different sediment grain sizes. Smaller individuals (<40 mm SL) preferred fine-grained sediments while larger individuals (≥ 40 mm SL) preferred coarse-grained sediments. Burying ability increased with size and all flounders avoided sediments that prevented burial. Subsequent laboratory experiments revealed that the presence of live prey (*Mya arenaria*) can over-ride sediment choice by winter flounder (50–68 mm SL) indicating the complexity of interrelated factors in habitat choice. © Published by Elsevier Science B.V.

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1. Introduction

Sediment structure is an important factor in the distribution pattern of many species of

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juvenile flatfish (Pihl and Van der Veer, 1992; Norcross et al., 1997; Abookire and Norcross, 1998) providing a refuge from predators and a resource of food (Ellis et al., 1997; Wennhage and Gibson, 1998). Some species of flatfish settle onto fine-grained sediments (Tanda, 1990; Keefe and Able, 1994) and laboratory experiments have demonstrated that several species can distinguish and select sediments based on grain size (Marliave, 1977; Tanda, 1990; Burke, 1991; Neuman and Able, 1998). Few attempts have been made to determine if fish size influences grain size selection (Moles and Norcross, 1995) and burying ability (Gibson and Robb, 1992), and rarely have both factors been investigated at the same time (Neuman and Able, 1998). Similarly, the role of food abundance in the distribution of flatfish has been suggested (Miller et al., 1991; Sogard, 1992; Jager et al., 1993; Gibson, 1994) but often field associations are confounded by the potential interaction between sediment qualities and food. Few laboratory experiments have been conducted on habitat choices related to food (Mattila and Bonsdorff, 1998; Neuman and Able, 1998; Wennhage and Gibson, 1998).

Young-of-the-year (YOY) winter flounder (*Pseudopleuonectes americanus*) spend their first year in relatively shallow inshore waters and are considered habitat generalists (Able and Fahay, 1998). Several investigators have reported that YOY winter flounder occur in higher densities on muddy sediments (Saucerman, 1990; Howell and Molnar, 1995; O'Conner, 1997) but others have found abundance is greater on sand (Sogard and Able, 1991; Goldberg et al., in review). To define substratum preference, we conducted a field survey of YOY winter flounder abundance and distribution in relation to sediment grain size characteristics in the Navesink River–Sandy Hook Bay estuarine system (NSHES), a recognized nursery area for this species (Phelan et al., 2000) (Fig. 1). We hypothesized that there were size-related shifts in habitat sediment selection. This relationship was tested subsequently in a series of laboratory experiments designed to examine size-related sediment selection and burying ability under controlled conditions. Finally, using a 50–68-mm SL size group, we tested the interaction of sediment grain-size selection and food availability on substratum choice using live prey (*Mya arenaria*).

2. Materials and methods

2.1. Field collections

YOY winter flounder and sediment samples were collected at 84 stations throughout the Navesink River–Sandy Hook Bay estuarine system (NSHES) in 1997 [for details see Stoner et al. (in press)]. One-meter beam trawl (3 mm mesh liner) surveys were conducted during late May and early July. All winter flounder were extracted from the samples, counted and measured for total length. Abundance was standardized to the natural log of the number of individuals 10 m^{-2}. For this investigation, YOY winter flounder were divided into two size groups (9–49 and 50–95 mm SL) based on findings that the diets of larger juvenile winter flounder (>50 mm) were ecologically distinct from smaller individuals in NSHES (Stehlik and Meise, 2000). Similarly, Stoner et al.

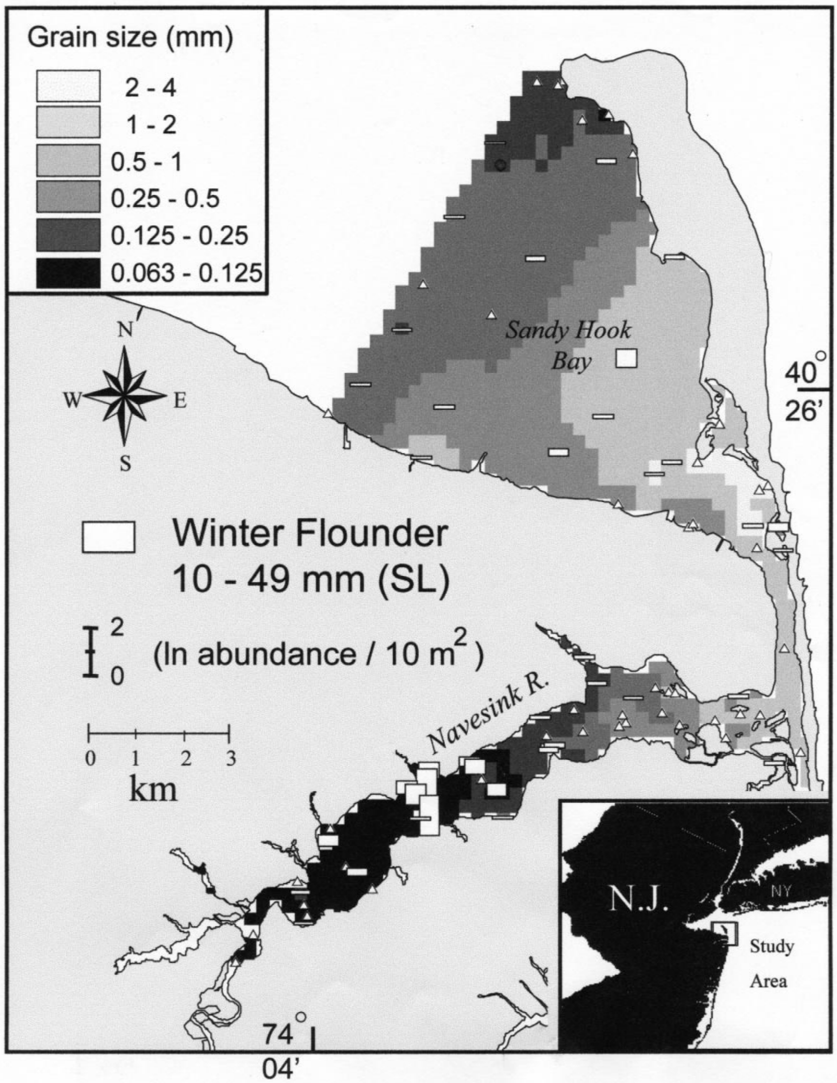

Fig. 1. Sediment grain size distribution in the Navesink River–Sandy Hook Bay estuarine system (NSHES) in New Jersey. Overlaid on the grain size distribution is the abundance (white bars) of winter flounder (10–49 mm SL) collected at each station in May 1997. Stations where no winter flounder were collected are illustrated by a white triangle.

(in press) determined that shifts in distribution of winter flounder were related to size. Each size group of winter flounder was scored as present or absent in each beam trawl collection at each station.

Sediment samples were collected in the middle of June with a weighted and frame mounted Van Veen grab or pole mounted Ekman grab. Core samples ($N = 3$; 3 cm diameter, 5 cm depth) were taken from each of the grabs for analysis of grain size by standard sieve fractionation (Folk, 1980). Product-moment statistics (McBride, 1971) were calculated for mean grain size and sorting coefficients. The sediment grain size data (mean diameter, mm) was mapped with ArcView GIS software [Arcview GIS 3.1 (1998); ESRI, Redlands, CA, USA] as continuous surfaces over a regional base map using inverse-distance weighted averaging. Grain sizes at each station were assigned to one of six 1-phi size classes (range = − 2.7–7 phi). The 84 survey stations were georeferenced and added to the same map. A grid cell size of 250 m was chosen for accuracy and image resolution.

The winter flounder presence/absence and sediment grain size diameter data were used in a logistic generalized additive model (GAM) to determine the probability of capturing fish in relation to sediment grain size. GAMS are nonparametric generalizations of logistic regression and were constructed with S-plus software (Math-Soft Inc., Seattle, WA, USA) using cubic spline smoothers and default degrees of freedom ($N = 4$) (Hastie and Tibshirani, 1990; Hastie, 1991; S-plus 4.5, 1997)

2.2. Laboratory studies

2.2.1. Collection and maintenance of experimental animals

YOY winter flounder of 15–69 mm standard length (SL) (18–83 mm TL) were collected from Sandy Hook Bay by beach seine (6 m; 6-mm mesh). The fish were transported to the Howard Marine Sciences Laboratory (Highlands, NJ, USA), separated into 10-mm SL size groups (i.e., 10–19, 20–29, etc.) and maintained in large aquaria with a continuous flow of filtered, ambient seawater pumped from Sandy Hook Bay. A natural light cycle (15–13 daylight h; June–September) was provided in all laboratories with a computer-controlled system of fluorescent lights. Temperature and salinity in the holding tanks over the course of the experiments were similar to those recorded in the experimental tanks (see Table 1). Rectangular holding aquaria (76 × 107 cm) were provided with 0.5 cm of a mixture of sediments consisting of equal parts of the five sediments used in the large arena sediment preference experiments (Table 2). Fish were

Table 1
Experimental conditions for sediment choice and buring ability experiments for young-of-the-year winter flounder[a]

Arena	Fish size (mm SL)	Temperature (°C)		Salinity (ppt)		Fish (total N)	Trials (N)
		Mean	Range	Mean	Range		
Small	15–19	16.4	14.7–18.1	25.3	25.2–25.4	24	6
	20–29	15.1	14.4–17.1	25.2	24.5–26.3	100	25
	30–39	16.2	14.7–17.5	25.5	25.0–26.1	92	23
Large	30–39	18.8	–	26.5	–	30	6
	40–49	20.0	19.5–20.3	27.3	26.8–27.8	80	16
	50–59	20.2	20.1–20.4	26.6	25.5–27.7	85	17
	60–69	20.7	20.1–20.9	26.4	25.5–27.2	65	13

[a] Small arenas (555 cm^2) held four fish per trial and large arenas (5075 cm^2) held five fish per trial.

Table 2
Sediment characteristics of substrata used in laboratory experiments

Sediment type	Mean [Phi (ϕ)]	Sorting coefficient (ϕ)	Mean diameter (mm)	Percent fines (%)
Muddy sand	1.86	0.93	0.27	4.45
Fine sand	2.26	0.52	0.21	1.47
Coarse sand	0.88	0.49	0.54	0.91
Fine gravel	−0.66	0.68	1.58	0.90
Gravel	−1.68	0.57	3.21	0.58

used for experiments within one week of capture and fed daily in the morning, ad libitum, on live brine shrimp (*Artemia* sp.) and chopped clam (*Spisula* sp.).

2.2.2. Experimental apparatus and sediments

We used two sizes of test arena for sediment preference and burying ability experiments. Small arenas (613 cm^2; 27 cm diameter × 19 cm deep) were used to test fish < 40 mm SL and large arenas (5688 cm^2; 85 cm diameter × 28 cm deep) for fish ≥ 30 mm SL. The centers of the arenas were made inaccessible to experimental fish by insertion of a perforated central hub (small = 8.57 cm diameter; large = 27.94 cm diameter) leaving the fish a ring-shaped surface area for movement (small = 555 cm^2; large = 5075 cm^2). Small arenas were perforated around their perimeter and placed in a water bath providing a water depth of 14 cm. Large arenas received ambient seawater around the periphery of the tank via a perforated tube placed just under the water surface. Water depth (22 cm) in the large arena was maintained with a central drainage standpipe located inside the central hub. In the small arenas, we used four azoic and inorganic sediments (fine gravel, coarse sand, fine sand, and muddy sand). In the large arenas we used the same four sediments and in addition we used gravel as a fifth sediment (Table 2). All sediments were commercially prepared except for the muddy sand, which was a mixture of 3/4 fine sand, and 1/4 finely ground vermiculite. As a result, the muddy sand mixture became slightly coarser in grain-size and more heterogeneous (sorting coefficient = 0.93) than the fine sand but had a higher percentage of fines (4.45%) and a softer, less cohesive texture, similar to muddy sands in the field. All sediments were rinsed with filtered seawater before use and arranged (2 cm deep) in equal-sized truncated wedges radiating from the central hub. The sediment arrangement made it less likely for a fish to rest on more than two sediments. In cases where a fish did rest on a two-sediment interface, the choice was determined by the sediment that was covered by the greater percentage of the fish body. Both arenas received ambient filtered seawater (15–21°C, 25–28 ppt; range for all experiments see Table 1) and were exposed to a natural photoperiod (see above).

2.2.3. Sediment selection and burying ability

For sediment selection and burying ability experiments, fish were fed ad libitum with live brine shrimp (*Artemia* sp.) and chopped clam (*Spisula* sp.) 1–2 h before the start of each experiment. The fish in the size group selected for a trial were transferred via a small bucket of seawater to the experimental aquaria. We tested four fish at a time in the small arenas and five fish at a time in the large arenas, randomly selecting and releasing a fish on each of the sediment types at the start of the experiments. Winter flounder were scored as present or absent on each type of sediment after 24 h. Burying ability (either buried or exposed) of the fish was also noted at that time. Fish were considered buried when $\geq$20–25% of the body surface was covered by sediment. Exposed fish had no sediment covering their bodies. Observations taken at 2 min, 1 h, 24 h, 48 h and 72 h for ten trials showed that selection and burial at 24 h were identical to those demonstrated over longer periods.

Three size groups of fish were tested in the small arenas: 15–19 mm SL (18–23 mm TL); 20–29 mm SL (24–35 mm TL) and 30–39 mm SL (36–47 mm TL). Fish 30–39 mm SL were also tested in the large arena to ensure that a change in selection was not related to the larger apparatus. We tested four size groups of fish in the large arenas: 30–39 mm SL (36–47 mm TL); 40–49 mm SL (48–59 mm TL); 50–59 mm SL (60–71 mm TL) and 60–69 mm SL (72–83 mm TL). The total number of trials per size and arena type ($N = 6$–25) varied depending on the number of fish available in a size group (Table 1). Each fish was only used once. Results were pooled over all trials within a size class and arena type and substratum selection was analyzed using a Pearson Chi-square (Zar, 1984). The null hypothesis was that substrata were chosen equally.

2.2.4. Sediment–food interaction

Experiments to examine the interaction between sediment choice and the presence of live prey, the soft-shell clam (*Mya arenaria*) were conducted in large arenas (see above) with winter flounder 50–68 mm SL. Winter flounder at this size range are benthivores and *Mya arenaria* is an important food item in this estuary (Stehlik and Meise, 2000) forming a natural predator–prey system. Also, winter flounder of this size were shown in the earlier sediment selection experiments to differentiate between fine-grained sediments (muddy sand, fine sand, and coarse sand) and coarse-grained sediments (fine gravel and gravel) giving us the opportunity to test differentially preferred substrata (S = fine sand and G = fine gravel) in combination with food presence. When prey were introduced to the arenas, they were spread uniformly on the surface of the side selected to receive prey and given an hour to bury, after which any unburied individuals were pressed gently into the sediment surface. One to two hours before the start of each trial, fish were fed ad libitum with live brine shrimp (*Artemia* sp.) and chopped clam (*Spisula* sp.). Single winter flounder (50–68 mm SL) were selected from the holding tanks and transported to the experimental tanks where they were gently released.

Two single-sediment experiments (S, $N = 6$ trials; G, $N = 6$ trials) were conducted where half the tank was randomly selected to receive prey. Individual winter flounder in each trial were exposed sequentially over 3 days to three different conditions: substratum alone, substratum with half the available surface area containing prey items (*Mya arenaria*; $N = 150$; 10–12 mm TL), and substratum with all the available surface area containing prey items (*Mya arenaria*; $N = 300$; 10–12 mm TL).

These experiments were followed by two two-sediment experiments where each of the two sediments was distributed across half of the arena bottom. In the first two-sediment experiment (S–G; $N = 6$ trials), *Mya arenaria* were initially placed on the nonpreferred sediment (G) and then on the preferred sediment (S). In the second two-sediment experiment (S–G; $N = 2$ trials), *Mya arenaria* were placed initially on the preferred sediment (S) and then on the nonpreferred sediment (G). Individual winter flounder were exposed sequentially over 3 days to three different conditions (see above). In these experiments, activity values were calculated over approximately 16-h intervals because the animals were generally quiescent after sunrise.

Low-light-sensitive video cameras were used to make continuous recordings of winter flounder movement (active, resting) over the observation periods. Feeding behavior, observed only during active time periods, was noted hourly, but was not quantified. During all trials, the mean percent time spent (time on substrata, %) both active and resting on each half of the available surface area, the mean percent time resting (time resting, %) out of the time spent on each half and the mean number of times the fish crossed over to the other half (line crossings) were measured and noted for each hour and averaged over the observation period. All sediments were removed and replaced between trials. Pooled trials from each experiment were analyzed using a Pearson Chi-square (Zar, 1984). The null hypothesis was that treatments within an experiment were chosen equally.

3. Results

3.1. Field collections

Fine-grained sediments were found in the middle and upper reach of the Navesink River and the outer margin of Sandy Hook Bay (Figs. 1 and 2). The median grain diameter of sediments in the study area ranged from 0.055 to 3.75 mm (4.17 to -1.91 phi ϕ). Only a few stations had substrata with grain diameters > 2 mm, and these were not used in the analysis. A total of 415 winter flounder, ranging in size from 8 to 95 mm SL, were collected in the two (May and July) surveys in NSHES in 1997. In May, the highest catches of winter flounder (10–49 mm SL) occurred in the fine-grained sediments of the Navesink River (Fig. 1). By July (Fig. 2), the larger animals (50–99 mm SL) were more widely distributed throughout the sampling area and were not as closely associated with the smaller grain sizes. By this time, substantial densities of winter flounder were collected in the apex and along the southern shore of Sandy Hook Bay (Fig. 2).

The general additive model (GAM) (Fig. 3) indicated that capture probabilities for small winter flounder (< 50 mm SL) were consistently high (range $= 0.23$–0.27) on fine sediments (0.055–0.5 mm) and declined on coarser grained substrata. In contrast, large fish (50–95 mm SL) had a low probability (range $= 0.05$–0.07) of being collected on fine sediments (< 0.25 mm). Capture probability of larger fish increased with grain size to a maximum at 1.0 mm and declined with coarser grain size.

3.2. Laboratory studies

3.2.1. Sediment selection and burying ability

Winter flounder exhibited a change in sediment grain size preference with growth. The smaller sizes (< 40 mm SL) consistently selected fine-grained sediments in the

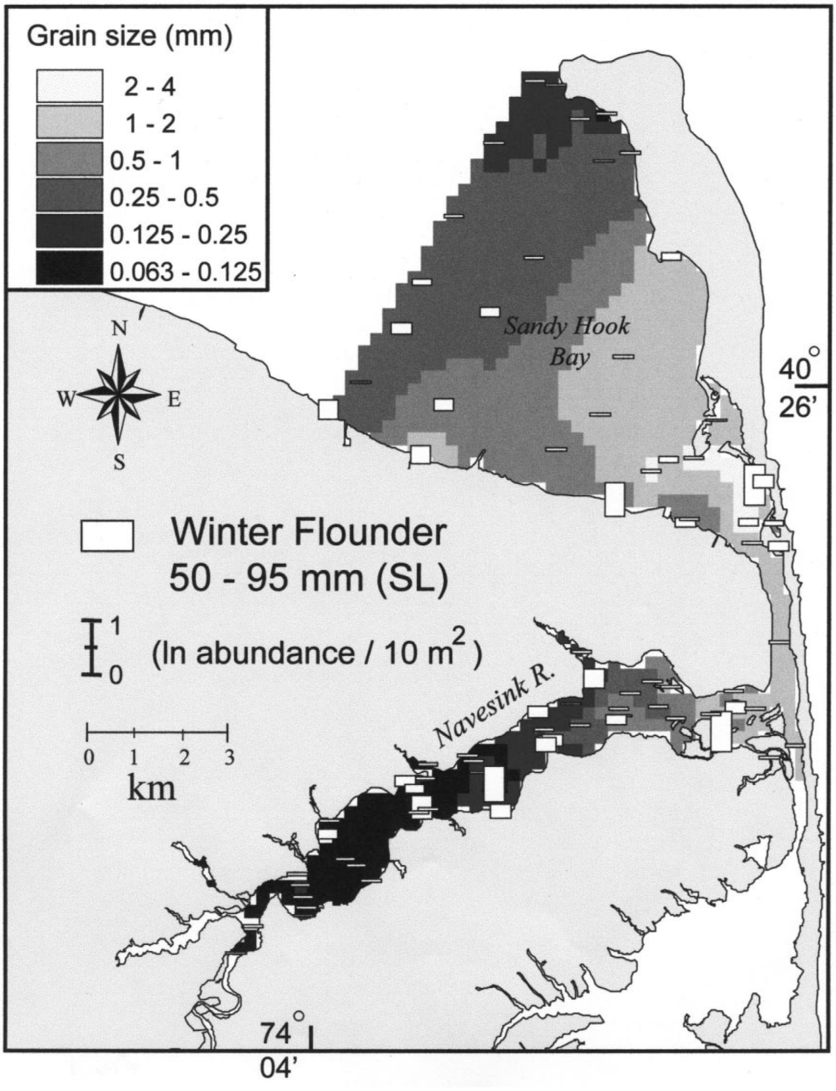

Fig. 2. Sediment grain size distribution in the estuarine system (NSHES) in New Jersey. Overlaid on the grain size distribution is the abundance (white bars) of winter flounder (50–99 mm SL) collected at each station in July 1997.

small arenas (Fig. 4a). Larger fish (40–49 mm SL) (Fig. 4b) showed a change in preference toward coarse sediments. Fish 50–59 mm SL had a preference for coarse-sand sediments and fish in the largest size class tested (60–69 mm SL) were positively associated with the three finer sediments (Fig. 4b). No fish in any size class selected gravel. The choice by 30–39 mm fish was not as strong in the larger arena as in the smaller arena but the trend was the same (Fig. 4a and b). While the shift in sediment

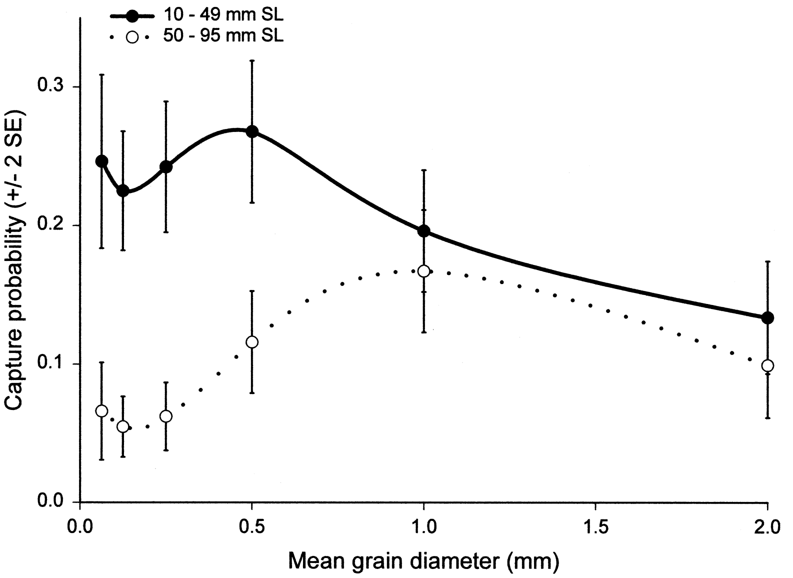

Fig. 3. Logistic generalized additive model (GAM) for the probability of capturing winter flounder in two size classes (10–49 and 50–95 mm SL) across the mean grain size diameter of sediments collected in the Navesink River–Sandy Hook Bay estuarine system (NSHES).

preference from fine to coarse substrata with size appeared clear, selection was not always statistically significant ($P > 0.05$). However, non-significant results occurred only where the number of trials was small ($N = 6$) (Table 1).

Burial among the various sediments types was also size-specific and followed the size shift exhibited in the sediment selection results (Table 3). The smallest size of winter flounder tested (15–19 mm SL) rarely buried and fish were often exposed and motionless during observation. Smaller fish (< 40 mm SL) that did bury had a preference for fine-grained sediment and larger fish (≥ 40 mm SL) buried more often in coarse-grained sediments. No winter flounder buried in the gravel sediment. The percent burial across all sediment types in each successive size class increased with an increase in size (Table 3). The relationship between winter flounder size and burying was highly correlated ($r^2 = 0.925$; $P = 0.001$).

3.2.2. Sediment–prey interactions

In the single-sediment experiments with prey, YOY winter flounder demonstrated a strong preference for sediments with food in both sand ($P < 0.001$) and gravel ($P < 0.01$) trials (day 2; Figs. 5a and 6a, respectively). No preference for either side of the arena in single-sediment experiments was observed when food was absent from the arenas (day 1; $P > 0.01$) or when food was present on both sides (day 3; $P > 0.1$), providing confidence that there were no laboratory artifacts in the choice of arena side on one sediment type. Percent of time spent resting on the two sides of the single-sediment arenas (days 1 and 3; Figs. 5b and 6b) was never significantly different

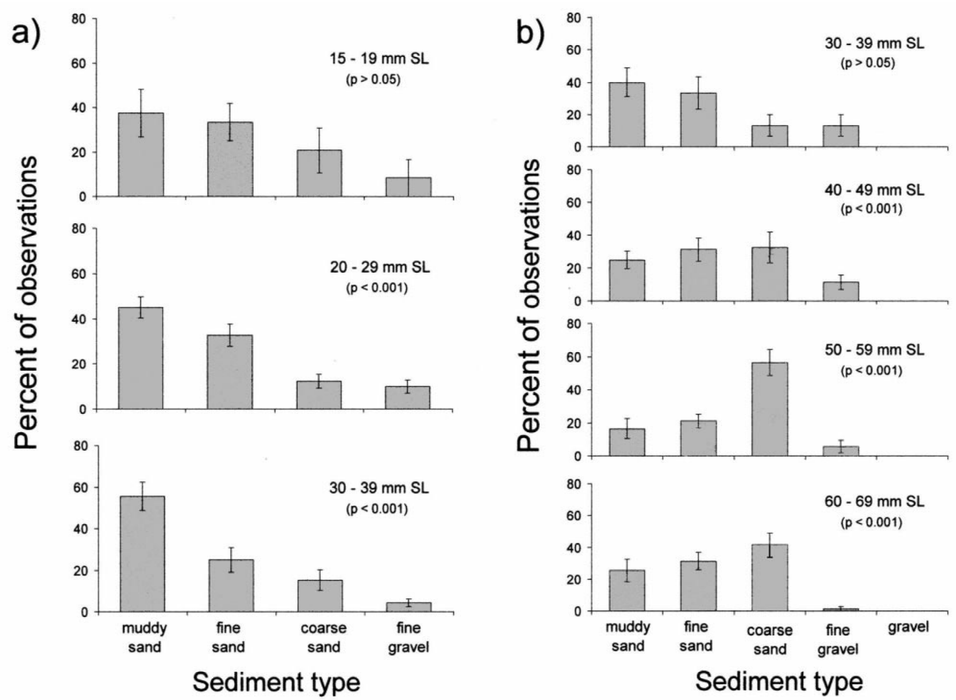

Fig. 4. Sediments selected by winter flounder 15–39 mm SL in (a) small laboratory arenas and winter flounder 30–69 mm SL in (b) large laboratory arenas. Statistical significance of the selection by a size group is illustrated in parentheses below the size. Error bars represent one standard error. For experimental details see Table 1.

($P > 0.1$), except on the gravel substratum when food was present on both sides (Fig. 6b; $P < 0.05$). Fish in this treatment rested for a longer period on the arena side with food added during the first day (Fig. 6b). One fish, resting for a long period of time, caused the apparent bias. We also noted that *Mya arenaria* on the fine gravel tended to

Table 3
Young-of-the-year winter flounder burial ability (number and percent) in different sediment types[a]

Arena size	Size (mm)	% Buried	% Buried in each sediment				
			MS	FS	CS	FG	G
Small	15–19	26.1	16.7	50.0	33.3	0.0	nd
	20–29	57.1	50.0	35.7	12.5	1.8	nd
	30–39	71.7	59.1	25.8	12.1	3.0	nd
Large	30–39	66.7	50.0	30.0	15.0	5.0	0.0
	40–49	93.8	25.3	33.3	32.0	9.3	0.0
	50–59	95.3	16.0	19.8	59.3	4.9	0.0
	60–69	97.1	25.0	30.9	42.6	1.5	0.0

[a] MS = Muddy sand; FS = fine sand; CS = coarse sand; FG = fine gravel; G = gravel. Gravel sediment was not tested in the small arenas. nd = No data.

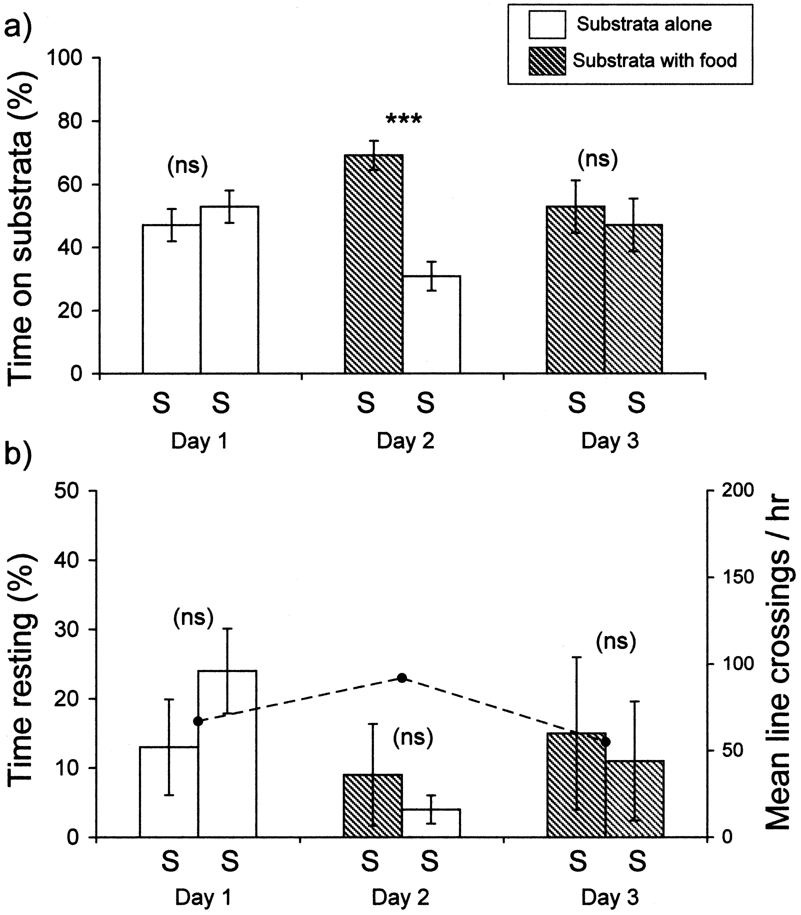

Fig. 5. Single-sediment (S = fine sand) experiments ($N = 6$ trials). Each pair of bars represents the two sides of an arena. Fish were exposed sequentially over 3 days to three experimental conditions: substratum alone, substratum with half the available surface area containing prey items (*Mya arenaria*; $N = 150$; 10–12 mm TL) and substratum with all the available surface area containing prey items ($N = 300$ *Mya*). (a) Percent time spent on substrata by winter flounder and (b) percent time resting on substrata and the number of line crossings by winter flounder (dashed line). Significance values (ns = Not significant, *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$) in parentheses refer to paired bars beneath them.

emerge from the sediment over time perhaps attracting fish to the side where the clams were present for the longest time. Locomotion was generally lower on the sand substratum (Fig. 5b; 55–92 mean line crossings/h) than on gravel (Fig. 6b; 87–150 mean line crossings/h); however, individual variation in movement (range = SE sand = 20.8–28.9; SE gravel = 35.1–45.7) was high.

In the two-sediment experiments, in the absence of food (day 1; Figs. 7a and 8a), the winter flounder showed a highly significant preference for fine sand over fine gravel as expected from previous experiments (Figs. 7a and 8a; $P < 0.001$ and < 0.01, respective-

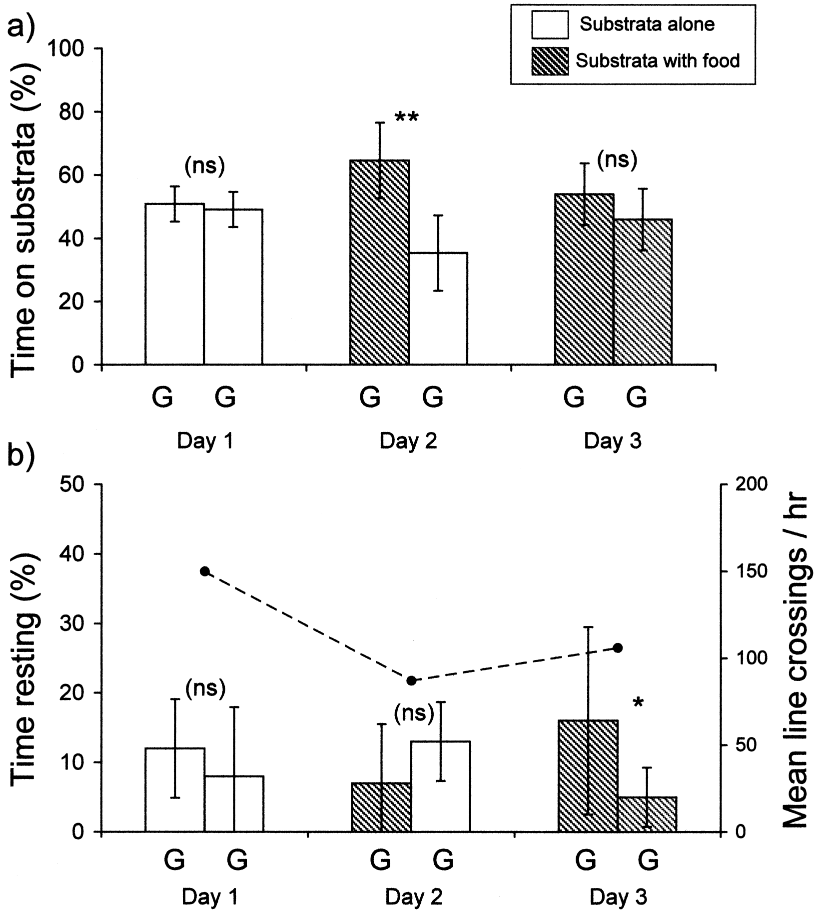

Fig. 6. Single-sediment (G = fine gravel) experiments (N = 6 trials). Each pair of bars represents the two sides of an arena. Fish were exposed sequentially over 3 days to three experimental conditions: substratum alone, substratum with half the available surface area containing prey items (*Mya arenaria*; N = 150; 10–12 mm TL) and substratum with all the available surface area containing prey items (N = 300 *Mya*). (a) Percent time spent on substrata by winter flounder and (b) percent time resting on substrata and the number of line crossings by winter flounder (dashed line). Significance values (ns = not significant, *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$) in parentheses refer to paired bars beneath them.

ly). However, when food was added to the gravel treatment (day 2; Fig. 7a), there was a significant shift ($P < 0.001$) to that side of the arena. When food was added to the sand side only (day 2; Fig. 8a), preference for sand over gravel was intensified and 93% of time was spent on sand. The response was mixed when food was present in both sediment types. In the experiment with food added to the gravel side first, no preference ($P > 0.05$) was observed (day 3; Fig. 7a). In the experiment with the food added to the sand side first, the fish preferred ($P < 0.001$) the arena side with the most recently added food (i.e., gravel) (day 3; Fig. 8a).

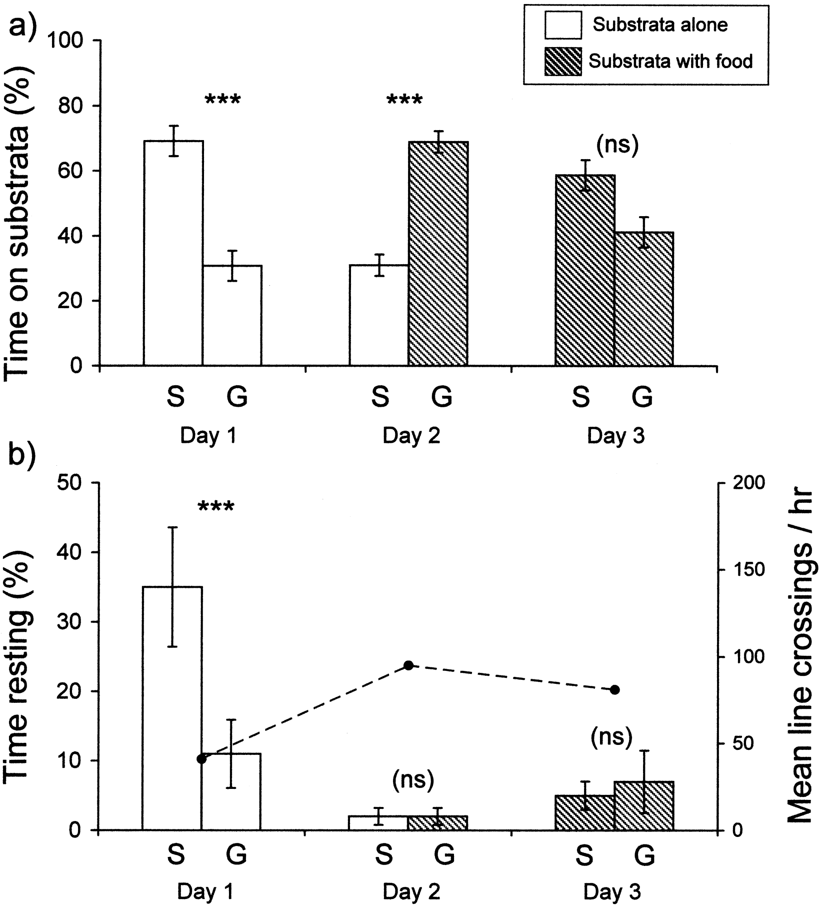

Fig. 7. Two-sediment (S = fine sand and G = fine gravel) experiments ($N = 6$ trials). Each pair of bars represents the two sides of an arena. Fish were exposed sequentially over 3 days to three experimental conditions: S and G alone, G containing prey items (*Mya arenaria*; $N = 150$; 10–12 mm TL) and S and G with all the available surface area containing prey items ($N = 300$ *Mya*). (a) Percent time spent on substrata by winter flounder and (b) percent time resting on substrata and the number of line crossings by winter flounder (dashed line). Significance values (ns = not significant, *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$) in parentheses refer to paired bars beneath them.

In both two-sediment experiments, the fish rested for a substantial proportion (42–46%) of the total time (sum of both arena halves) when food was not present in the arena (day 1; Figs. 7b and 8b). When food was present in the gravel or on both sides (days 2 and 3; Fig. 7b) average resting time decreased to $< 12\%$ of the total time and there were no significant differences in the amount of time spent resting on the two sediments. In contrast, when food was present only in sand (day 2; Fig. 8b), the fish rested for 30% of the time, primarily on the sand habitat. Concordant with the observation of decreased resting time in the presence of food, the number of times that fish crossed the boundary

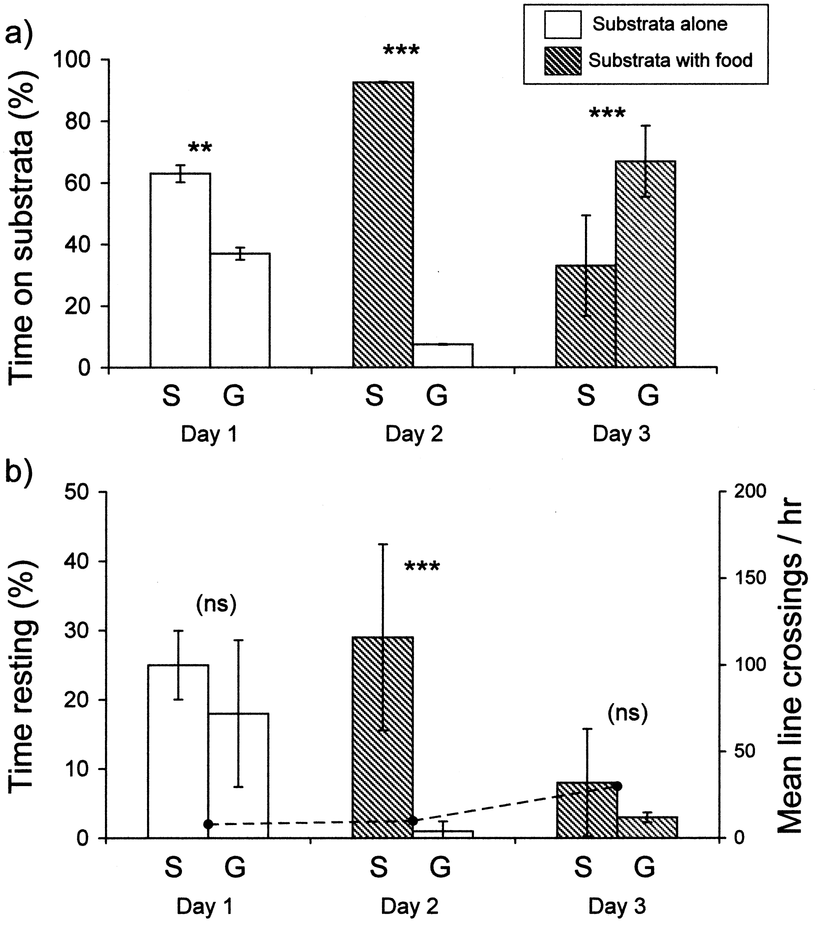

Fig. 8. Two-sediment (S = fine sand and G = fine gravel) experiments ($N = 2$ trials). Each pair of bars represents the two sides of an arena. Fish were exposed sequentially over 3 days to three experimental conditions: S and G alone, S containing prey items (*Mya arenaria*; $N = 150$; 10–12 mm TL) and S and G with all the available surface area containing prey items ($N = 300$ *Mya*). (a) Percent time spent on substrata by winter flounder and (b) percent time resting on substrata and the number of line crossings by winter flounder (dashed line). Significance values (ns = not significant, *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$) in parentheses refer to paired bars beneath them.

between the two sediments (mean line crossings/h) generally increased in the presence of food (days 2 and 3; Fig. 7b). The index of locomotion (mean line crossings/h) was 2–3 times higher in the experiment with food added to gravel first (Fig. 7b) than in the experiment where food was added to sand first (Fig. 8b), but there was considerable variation (range = SE experiment 1 = 320.0–838.1; SE experiment 2 = 35.9–172.6) among the individuals. Fish movements were also more variable (e.g., stop–start, turning, nipping, etc.) in the presence of food than without food (swimming in one direction).

4. Discussion

Habitat descriptions for flatfish often include sediment characteristics because of their close association with the bottom (Scott, 1982, Burke et al., 1991; Norcross et al., 1995, 1997). Jager et al. (1993) found that sediment was the most important factor explaining differences in catch densities for 0-group plaice (*Pleuronectes platessa*) with densities decreasing abruptly when the sediment contained more than a 10% mud fraction. In contrast, the distribution of sole (*Solea solea*) was highly dependent on the presence of a homogeneous substratum of median grain size diameter of less than 0.20 mm (Rogers, 1992). YOY winter flounder are considered habitat generalists (Able and Fahay, 1998) because they are collected on a wide variety of substrata. Sogard (1992) found a positive association of abundance with sand while others (Saucerman, 1990; Howell and Molnar, 1995) found that YOY winter flounder were most abundant on muddy sediments.

Conflicting evidence about sediment grain size preference in winter flounder may have resulted from pooling across all sizes of age-0 fish. In our study, we found significant size-related patterns in sediment selection by YOY winter flounder. In both the field and in laboratory experiments, fish <40 mm SL selected fine-grained sediments (<0.5 mm) while fish ≥ 40 mm SL selected coarse-grained sediments. Size-related shifts in habitat use for other flatfish species have been observed in Georgia estuaries (Rogers et al., 1984), California coastal waters (Kramer, 1991), and in a Louisiana bay (Allen and Baltz, 1997). In laboratory studies, four species of juvenile Pacific flatfishes (Moles and Norcross, 1995) demonstrated strong sediment selection but only juvenile starry flounders (*Platichthys stellatus*) selected larger particles with increasing size. In a related study in our laboratory (Stoner et al., in press), models of winter flounder habitat association for the Navesink River–Sandy Hook Bay estuarine system, showed that YOY winter flounder, <55 mm TL, were more likely to be associated with fine-grained sediment rich in organic content. However, sediment characteristics appeared to be less important to larger individuals (55–130 mm TL) which frequently occurred in shallow vegetated habitats (primarily sea lettuce, *Ulva lactuca*). Sediment grain size is an important factor in the habitat choice of flatfish but habitat designations need to consider shifts in habitat preference based on size.

Size-related changes in sediment grain size preferences paralleled results in winter flounder burying capacity. Fish buried more often with increasing size and buried in coarser sediments, a trend seen in other flatfish species (Tanda, 1990; Keefe and Able, 1994; Minami et al., 1994; Moles and Norcross, 1995). Gibson and Robb (1992) demonstrated a clear relationship between fish body length, sediment grain size and the extent to which juvenile plaice (*Pleuronectes platessa*) bury in laboratory experiments. They assumed that larger fish were able to exert more force and thereby utilize coarser sediments than smaller fish. We found that the smallest winter flounder tested (15–19 mm SL) did not bury as often as larger fish and that no fish buried in the coarsest sediment tested (gravel). Other flatfish laboratory studies have found a failure of small fish to bury in fine sediments (Gibson and Robb, 1992; Neuman and Able, 1998).

Burying ability is believed to have survival advantages as it makes YOY flatfish less vulnerable to predators (Tanda, 1990) but burying in sand may provide only a partial refuge from predation, because natural predators have evolved effective methods of foraging for buried prey (Ansell and Gibson, 1993). Predator type can determine whether a newly settled flatfish successfully avoids predation by burying in the substrata or by fleeing (Keefe and Able, 1994; Manderson et al., 1999). Recently settled winter flounder do not achieve a size refuge from sand shrimp (*Crangon septemspinosa*), which is a major predator, until the flounders reach 17 mm SL (Witting and Able, 1993). Since sand shrimp often bury during the day (Manderson et al., 1999), we speculate that burial by small flatfish may not always be necessary to avoid predation. The smaller winter flounder tested in our experiments exhibited cryptic coloration and limited movements in the test arenas (personal observation) making them difficult to locate. The effect of cryptic coloration on survival of wild flatfish has not been examined experimentally (Ellis et al., 1997) but cryptic coloration has been shown experimentally to reduce predation mortality in salmonids (Donnelly and Whoriskey, 1991).

Winter flounder substrate preference in the laboratory was strongly influenced by the presence of prey. Size-related habitat preference may be related to abundance of suitably sized prey, which may also be associated with certain sediment characteristics. Jager et al. (1993) concluded that the relationship between plaice (*Pleuronectes platessa*) habitat selection and the abundance of preferred food items was probably indirect. In laboratory experiments, Wennhage and Gibson (1998) determined that plaice spent significantly more time on a sediment with benthic food than on one without food. Summer flounder (*Paralichthys dentatus*) selected sand whether prey was present or absent but southern flounder (*Paralichthys lethostigma*) preferred mud when prey was present and showed no preference when prey was absent from the substrate (Burke, 1991). Other investigations on flatfish sediment preference have found inconsistencies between field sediment choice and laboratory sediment choice (Wyanski, 1990; Keefe and Able, 1994; Norcross et al., 1995) prompting speculation that prey availability in the field may be a confounding factor in habitat selection. Mean sediment grain size and organic content are inversely related sediment characteristics in NSHES (Stoner et al., in press) and benthic food items tend to be associated with high organics (Shaw and Jenkins, 1992). In NSHES, the distribution of the benthos and abundance of winter flounder are correlated with several abiotic variables such as temperature, salinity, depth, sediment organics, labile carbon, and redox potential (Stoner et al., in press; Manderson et al., unpublished data). Clearly, more research is needed to elucidate this complex relationship.

Habitat selection is a multifactorial problem (Allen and Baltz, 1997; Stoner et al., in press). Difficulty in characterizing habitat for flatfish has been exacerbated by pooling animals over year classes or size intervals. While size-related shifts occur in continua, we have observed that YOY winter flounder need to be considered in several groups, and the same may be true for other species. Sediment grain size is only one part of a complex interaction among biotic and abiotic factors involved in habitat selection (Rogers, 1992; Gibson, 1994).

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